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The Enigmatic Biology of the Ichneumonid Subfamily Lycorininae

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Abstract.—Females of *Lycorina apicalis* Cresson and *L. marvini* Gauld (Ichneumonidae: Lycorininae) were dissected and found to have pedunculate eggs with an 'anchor' at the tip, similar to those of Tryphoninae. Several differences are noted between Tryphoninae and Lycorininae and thus no close relationship is indicated. Observations of *L. apicalis* reared from a larva of *Omiodes indicata* (Lepidoptera: Crambidae) demonstrate that this species is a koinobiont that finishes its development as an ectoparasitoid. However, we were unable to locate the early larval stages of the parasitoid on the exterior of the host.

Key words.—*Lycorina*, *Omiodes*, Crambidae, egg morphology, koinobiont, ectoparasitoid, Costa Rica

The Lycorininae is a small subfamily of Ichneumonidae composed of 28 species classified in a single genus, *Lycorina* Holmgren (Yu and Horstmann 1997). The monophyly of the group is supported by several unusual synapomorphies, including the unique metapleural catch (Gauld 1984), raised and clearly defined triangular areas on tergites II–IV, and possession of a large triangular subgenital plate in the female which is weakly sclerotized in the central part. The group is cosmopolitan, but unlike most other subfamilies of Ichneumonidae it is most species rich in the tropics and the southern hemisphere (Yu and Horstmann 1997). The phylogenetic relationships of the Lycorininae are poorly understood. Townes, in his various reclassifications of the Ichneumonidae initially placed it as a tribe in the Banchinae (Townes and Townes 1951), later as a genus in the banchine tribe Glyptini (Townes and Townes 1966) and finally, on the basis of information about the larva, as a distinct subfamily next to the Banchinae (Townes 1970). However, the characters supporting a relationship with the Banchinae appear to be symplesiomorphies (Gauld 1984) so the phylogenetic placement of this group remains uncertain.

Compounding this uncertainty is the fact that very little is known of the biology of the group, and it is not known for certain whether species are ecto- or endoparasitic, koinobiont or idiobiont (Gauld 1997). Although there are comparatively few rearing records, the focal host range of lycorinines seems to be the weakly concealed larvae of microlepidopterans. Some species from north temperate regions have been reared from pyralid leaf-rollers and leaf-tiers (Doerksen and Neunzig 1974, Finlayson 1976), and from tortricids (Chao 1980). Of the eight species found in Costa Rica only one, *L. apicalis*, has been reared. Previous host records for this species include an undetermined species of *Lamprosema* Hübner (Crambidae: Pyraustinae) (Gauld 1997) and the prepupa of *Ethmia catapeltica* Meyrick (Ethmiidae) (Janzen and collaborators: *http://janzen.sas.upenn.edu/*). Recently we reared this same species from *Omiodes indicata* (Fabricius) (Cram-

bidae: Pyraustinae), collected in May, 1996, in leaf-rolls of beans (*Phaseolus vulgaris* L.), in a field located in Turrialba, Costa Rica.

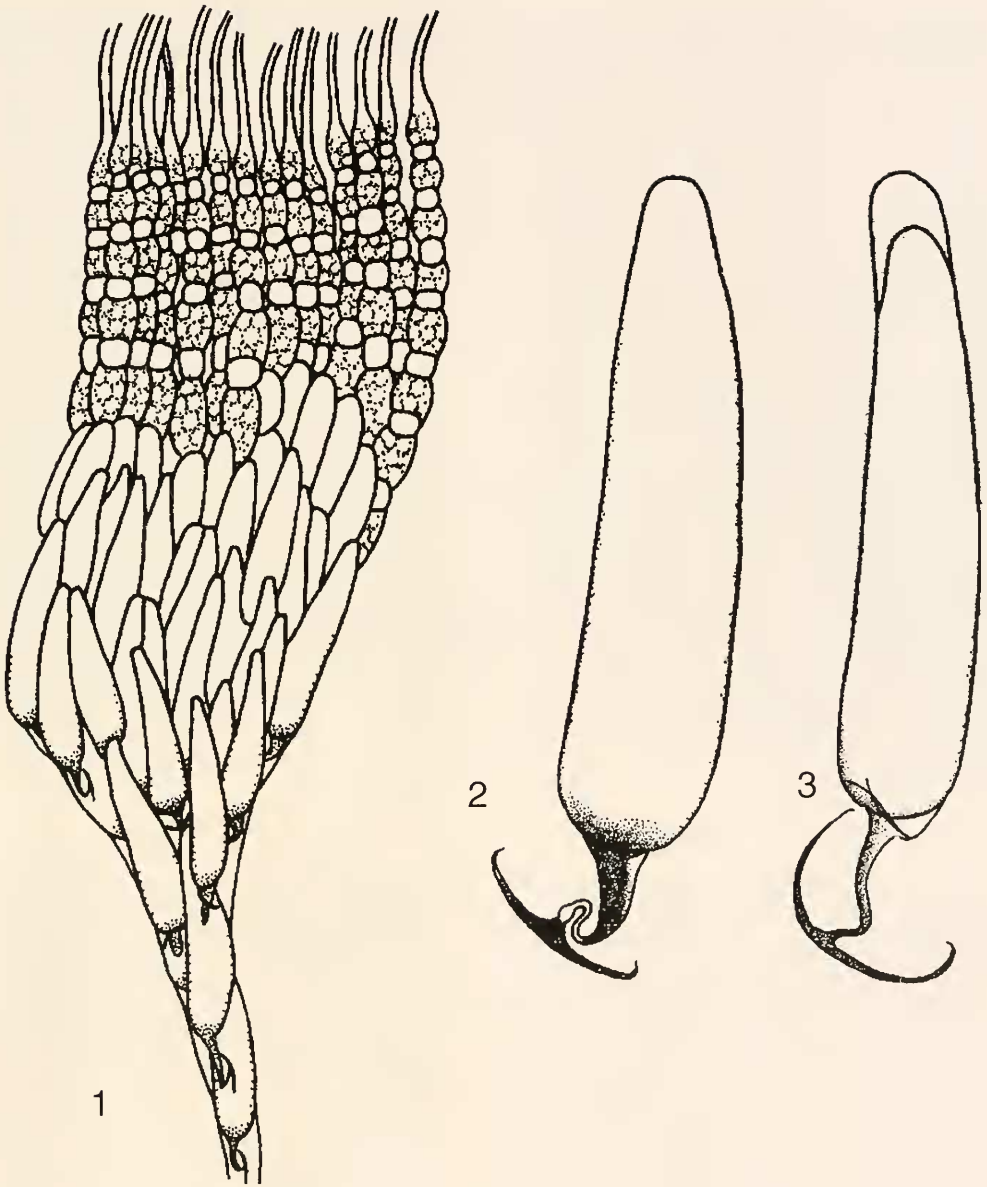
The head capsule of the final instar larva is enigmatic, possessing features of both ectoparasitic and endoparasitic species. For example, the mandibular teeth are denticulate, similar to some other ectoparasitic ichneumonids such as Tryphoninae and Cryptinae (Finlayson 1976, Short 1978, Chao 1980, Gauld 1997). Nonetheless, some endoparasitic braconids such as Microgastrinae, which emerge from their hosts in the final instar in order to complete their development by feeding externally, have a similar mandibular tooth (Capek 1973). On the other hand, in contrast to many ectoparasitoids, the larvae of Lycorininae lack a distinctive labral sclerite, have a disc-like antenna, and the spiracle lacks a closing device, all of which suggest that the larva is possibly endoparasitic (Gauld 1997).

In this note we present some new observations on the biology and anatomy of these enigmatic insects, which complement recent observations on a European species of *Lycorina* (Shaw 2004). Voucher specimens are deposited in the Insect Museum of the University of Costa Rica (IM-UCR, San Pedro) and in the National Biodiversity Institute (INBIO, Santo Domingo).

Egg Morphology

Four female specimens of *L. apicalis* Cresson and two of *L. marvini* Gauld, (collected in Malaise traps from various sites in Costa Rica), were dissected to observe the morphology of the ovaries and eggs. In both species the eggs are elongate-oval, with a chitinized chorion, and lightly sclerotized at the apex in *L. apicalis*. Remarkably, the eggs of both species have a long, thin, and flexible peduncle with an "anchor" at the apex, although the exact form of the anchor varies between the two species (Figs. 2–3). Possession of stalked eggs with an anchor-like end is elsewhere, in Ichneumonidae, only known within the subfamily Tryphoninae (Bennett 2002). However, there are several notable differences between the eggs of Lycorininae and Tryphoninae. Those of the latter subfamily are much larger (1.06–0.24 mm in length, avg. = 0.64; 0.41–0.09 mm in width, avg. = 0.27; data from Iwata, 1958, based on 10 species in 5 tribes) compared with the small eggs of *L. apicalis* (0.5 mm in length; 0.1 mm in width) and *L. marvini*: (0.6 mm in length; 0.1 mm in width), and tryphonine eggs have a strongly sclerotized chorion (Iwata 1960, Kasparyan and Tolkanitz 1999). Moreover, in many tryphonines the anchor, not the egg, travels down the lumen of the ovipositor (Kasparyan 1981). The egg is attached externally to the host by the anchor which is pushed through the host's cuticle by the ovipositing female ichneumonid (Simmonds 1947, Baltensweiler and Moreau 1957, Pschorn-Walcher 1967, Beingolea and Vásquez 1994). In many female tryphonines an egg is visible beneath the base of the ovipositor. We have examined over 100 individuals of *Lycorina* collected in Costa Rica but never observed an egg in a similar situation, which suggests that perhaps the egg travels down the lumen of the ovipositor in the normal ichneumonid manner.

The only published study of the eggs of species in this subfamily (Iwata 1958) described the eggs of the Palaearctic species, *L. triangulifera* (Holmgren), as being leech-shaped. Although Iwata's description differs from our observations, Shaw (2004) has recently found that the eggs of *L. triangulifera* do in fact have an anchor, which agrees with our results. Our observations are similar to those of Iwata (1960) in that the ovaries of all lycorinine species are characterized by having high numbers of ovarioles: *L. apicalis* (10–19 per ovary) (Fig. 1); *L. marvini* (13–27 per ovary); *L. triangulifera* (18–25 per ovary), with many small eggs, 13–23 per ovary in *L. apicalis*,



Figs. 1–3. Ovaries and eggs of *Lycorina*. 1, Ovary of *L. apicalis*. 2, Egg of *L. apicalis*. 3, Egg of *L. marvini*.

30–40 per ovary in *L. marvini* and 32–64 per ovary in *L. triangulifera*.

The similarity in egg structure among the three species that have been observed suggests that lycorinines share a similar developmental biology. The pedunculate, anchored egg of Tryphoninae has been considered to be an adaptation for ectoparasitism (Bennett 2002), but several observations suggest that lycorinines are endoparasitoids, or at least begin their development as endoparasitoids. The form of the ovaries of *Lycorina* are more similar to those of endoparasitic koinobiont ichneumonids than they are to those of ectoparasitic koinobionts or idiobionts. The data of Iwata (1960), who examined 1,397 specimens representing 376 species of Ich-

neumonidae, suggest that the ovaries of idiobionts and ectoparasitic koinobionts tend to have rather few ovarioles (idiobionts: 2–15 per ovary; ectoparasitic koinobionts: 3–8 per ovary) and a reduced number of relatively large, mature eggs (idiobionts: 2–14 per ovary; ectoparasitic koinobionts: 3–10 per ovary). In contrast, endoparasitic koinobionts tend to have a large number of ovarioles (3–59 per ovary) and a large number of relatively small, mature eggs (24–111 per ovary). In the three species of *Lycorina* in which the ovaries have been described, there are 10–27 ovarioles per ovary, and the mature eggs are relatively small and numerous (13–64 per ovary). Thus, both the structure of the ovaries and the size of the eggs suggest that lycorinines are endoparasitic koinobionts. However, it should be kept in mind that the above comparisons do not take into account phylogenetic dependence (e.g. in Tryphoninae, the low number of ovarioles and eggs could simply be the ancestral condition).

Larval Development

In the specimen of *L. apicalis* that we reared from a larva of *Omiodes indicata*, the parasitoid larva was not observed until eight days after the caterpillar had been collected. At that point the larva of *L. apicalis* was observed feeding as an external parasitoid, just as the caterpillar was beginning to spin its cocoon. Although we cursorily examined the host larva prior to this, we failed to notice any external parasitoid or externally positioned egg. The adult parasitoid emerged 21 days after having eaten the host. The remains of the host were examined under a dissecting microscope to see if there were remains of an externally deposited egg, but none were found.

Although the above observations are consistent with development being initially endoparasitic, the recent discovery that the egg of *L. triangulifera* is deposited through the anus of the host (Shaw 2004) explains why we failed to observe young larvae, and also suggests that early development could possibly occur as an ectoparasitoid in the hindgut. Both our results and those of Shaw (2004) demonstrate that lycorinines are koinobionts, and our observations show that development is completed as an ectoparasitoid. However, whether the young larvae are ectoparasitic (presumably in the hindgut), or endoparasitic, remains to be demonstrated.

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